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ORIENTATION OF THE ROTATION-AXIS RELATIVE TO GRAVITY: ITS INFLUENCE ON NYSTAGMUS AND THE SENSATION OF ROTATION

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JOINT REPORT

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Research Report

ORIENTATION OF THE ROTATION-AXIS RELATIVE TO GRAVITY: ITS INFLUENCE ON NYSTAGMUS AND THE SENSATION OF ROTATION*

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SUMMARY PAGE

THE PROBLEM

To estimate the influence of changing orientation relative to gravity on responses usually presumed to be controlled by semicircular canal stimulation.

FINDINGS

Continual reorientation relative to gravity during semicircular canal stimulation has profound influence on the nystagmus and subjective reactions usually attributed to semicircular canal stimulation. During rotation about a horizontal axis, nystagmus and sensations of rotation are lengthened. When rotation about the axis stops, reactions are greatly suppressed. The latter aspect of the results will be essential to the interpretation of responses as subjects make "natural" head movements while moving about in the plane of rotation to "simulate" conditions of a rotating space station.

ACKNOWLEDGMENTS

The author gratefully acknowledges the cooperation of the individuals from Gallaudet College and the U. S. Naval School Pre-Flight who served as subjects in this experiment.

INTRODUCTION

The semicircular canal system alone cannot indicate the orientation of the axis of rotation of the head relative to gravity, according to classical concepts of the mechanics of the canals (9,45). This function may be served by the otolith system. If a particular set of semicircular canals is maintained in the plane of rotation, a given angular acceleration would deliver equivalent stimuli to the cupula-endolymph rings irrespective of the particular orientation of the rotation-axis relative to gravity and irrespective of the magnitude of gravity, assuming that the semicircular canals respond solely to change in angular momentum. Hence, this issue is of significance to a number of conditions to be encountered in space ventures, including weightlessness. The present study compares vestibular responses, subjective phenomena and nystagmus, obtained in two situations: one in which the rotation-axis was vertical, i.e., aligned with gravity, and one in which the rotation-axis was horizontal (see Figure 1).

The testing device customarily used, some variation of the Bárány chair, is a vertical-axis device, and when the head is fixed to the rotary structure, the otolith planes of the utricle and saccule are not reoriented relative to gravity during or after rotation. Hence during rotation, with the head centrically located, sensory information from the otolith system neither denies nor confirms the rotation signaled by the canals*.

On the other hand, rotation about a horizontal-axis produces continuous reorientation of the otolith planes relative to gravity. In this situation, the canals and otoliths signal a coplanar change in angular position during angular acceleration. If the rotation continues at constant velocity, the cupula may return to a nonstimulating position by virtue of its elasticity, but the otoliths may continue to signal the constantly changing angular position relative to gravity. When rotation is stopped, the canals respond as though rotation had commenced in the opposite direction, but the change from continuous otolith reorientation to fixed orientation may conflict in this special case with the semicircular canal post-rotational response. Hence, while stimulation of the semicircular canals may be identical under these two circumstances, stimulation of the otolith system (and other body organs) would be quite different (cf. 44).

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*unless we assume, as Lowenstein (25) suggests, that the product of angular acceleration times radius is sufficient to stimulate the otoliths, in which case they would reinforce canal input during angular acceleration when the axis of rotation is vertical.

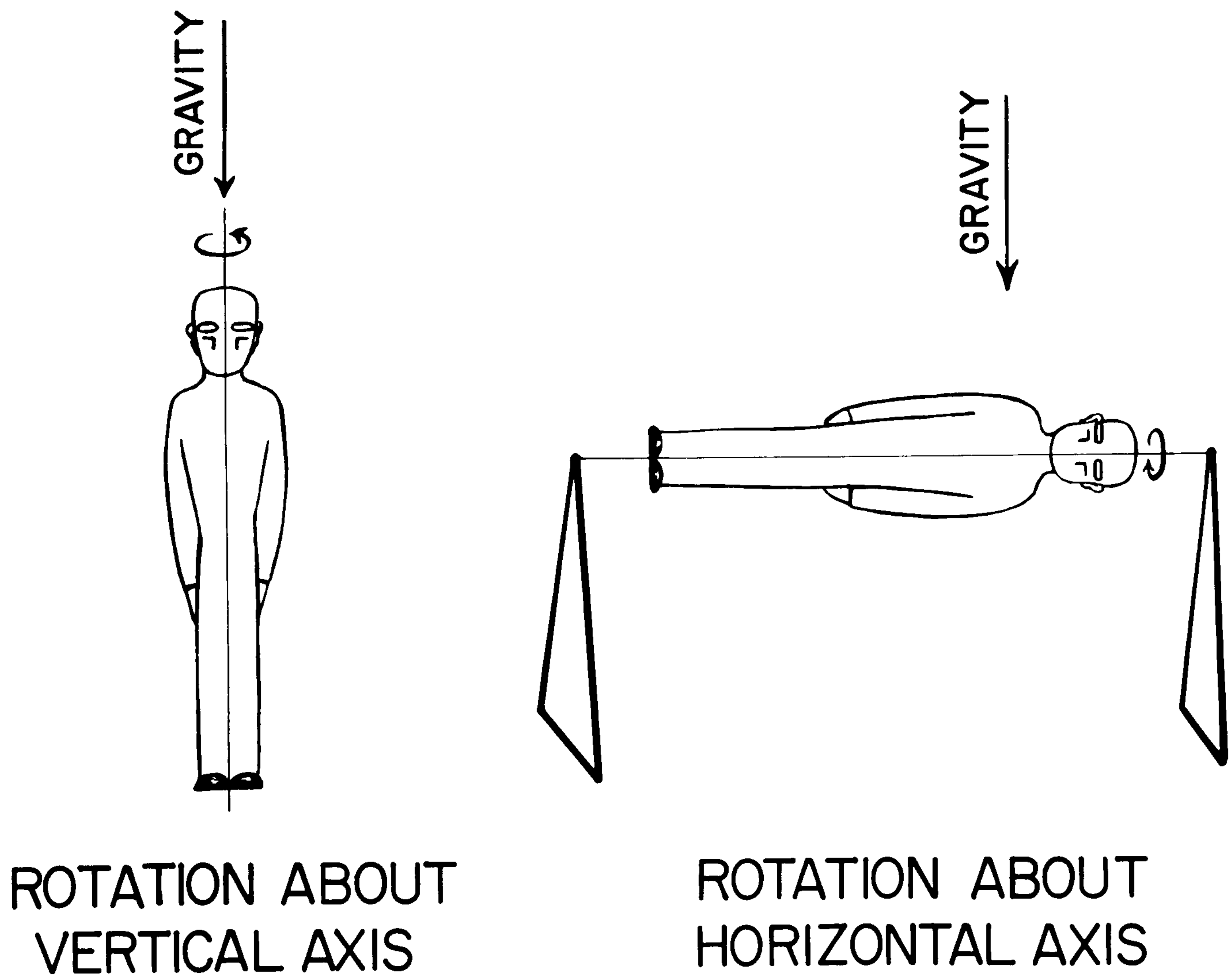

Figure 1

Illustrating the Two Axes of Rotation Used in the Experiment. Horizontal Semicircular Canals Were in the Plane of Rotation in Both Situations, but Continuous Reorientation of the Otolith Planes Occurred Only When the Axis of Rotation Was Horizontal.

Fundamental to the inference that the response of the cupula-endolymph system would be independent of the orientation of the rotation axis relative to gravity is the assumption that the cupula and endolymph have very nearly the same specific gravity (5). Various physical characteristics which would determine the physical responses of the vestibular receptors to linear and angular accelerations have been clearly presented in the past (10,27,38,39), usually in connection with the analysis of possible effects of centrifugal force on the cupula response when subjects were positioned away from the center of rotation. Although these analyses have usually led to the conclusion that the canal response should not be altered by those linear acceleration vectors which do not induce a change in angular momentum, various experiments (2,8,11,12,22,23,24,29) have indicated an effect of linear acceleration on responses ordinarily considered to be regulated by cupula displacement. These results may be indicative of a cupula which is sensitive, though perhaps not very sensitive, to linear acceleration, or otoliths which are sensitive to high magnitude angular acceleration (25), or they may signify modulation of cupula neural input by other body systems, e.g., the otoliths (35). On the other hand, several experiments have shown little change in results when linear acceleration was added (14,39).

The present report is relevant to these issues and compares the results obtained from normal subjects with results obtained from individuals believed to be without labyrinthine function (L-D subjects).

PROCEDURE

SUBJECTS

Subjects were twelve men with normal vestibular function and eleven men with bilateral loss of inner ear function as indicated by caloric tests, rotation tests, and audiometric examination.

APPARATUS

The rotary apparatus is a device similar to the electric posture table described by Aschan, et al. (1). It consists of two independently rotating frames, each driven by a 1/3 HP DC motor, which may be rotated simultaneously or singly. The axis about which the outer frame rotates produces head over heels rotation of human subjects. However, in the present experiment this frame was fixed in either of two positions, one vertical and the other horizontal, and only the inner frame was rotated to produce controlled stimulation. The inner frame is pivoted to the outer frame and permits rotation about the cranio-caudal axis. The subject is securely strapped to the inner frame. Angular accelerations and final angular velocity can be preset for either frame by dials on the control panel. The maximum constant angular velocity and constant angular acceleration of the inner frame are 68 deg/sec and 26 deg/sec^2, respectively. These were the stimulus magnitudes used throughout the present experiment. Maximum angular velocities and accelerations of the outer frame are 18 deg/sec and 6 deg/sec^2, but this frame was merely prepositioned in the present study, and these control features of the outer frame were not utilized.

Slip rings from the inner to the outer frame and another set from the outer frame to the support structure permit recording of corneo-retinal potentials and other response variables.

Subjects were secured to a padded bed on the inner frame by means of a head-rest, adjustable side pieces, an adjustable footrest, and safety straps across the feet, thighs, chest, shoulders, and head. In addition, an orthopedic brace, designed to immobilize the head relative to the body, was secured to the inner frame. The supports, straps, and orthopedic brace are visible in Figure 2.

Electrodes taped near the outer canthus of each eye were used to record the horizontal component of eye movements by virtue of the corneo-retinal potential, amplified by a Sanborn Model 350-1600 preamplifier (time constant 1.5 sec). Eye movements, the angular velocity of the inner frame and a position marker for the inner frame were recorded.

METHOD

Each subject was given two tests with the axis of rotation vertical and two tests with the axis of rotation horizontal. The first of the two tests with each axis-orientation was clockwise (CW) rotation, i.e., rotation to the subject's right, and the second was counterclockwise (CCW). As indicated before, starts and stops were accomplished by angular accelerations of 26 deg/sec^2 and angular velocities of 68 deg/sec were attained. Constant angular velocities were maintained during vertical-axis tests for ninety seconds. In the horizontal-axis tests, constant angular velocities were maintained for several minutes because of the greater persistence of nystagmus reactions about this axis.

During and after each period of rotation, nystagmus was recorded. Between trials, subjects were asked to describe the perceptual experiences produced by the test situations. Vision was excluded during all trials by darkening the experimental room and by a foam rubber mask which prevented vision without touching the eyeballs or eyelashes. Subjects were instructed and frequently reminded to keep their eyes open throughout each test.

RESULTS

NORMAL SUBJECTS

Tests with the axis of rotation vertical produced the usual results. In general, nystagmus and sensations of rotation persisted twenty-five to forty seconds beyond the termination of the angular accelerations used to start and stop the rotation. Nausea was absent during these tests.

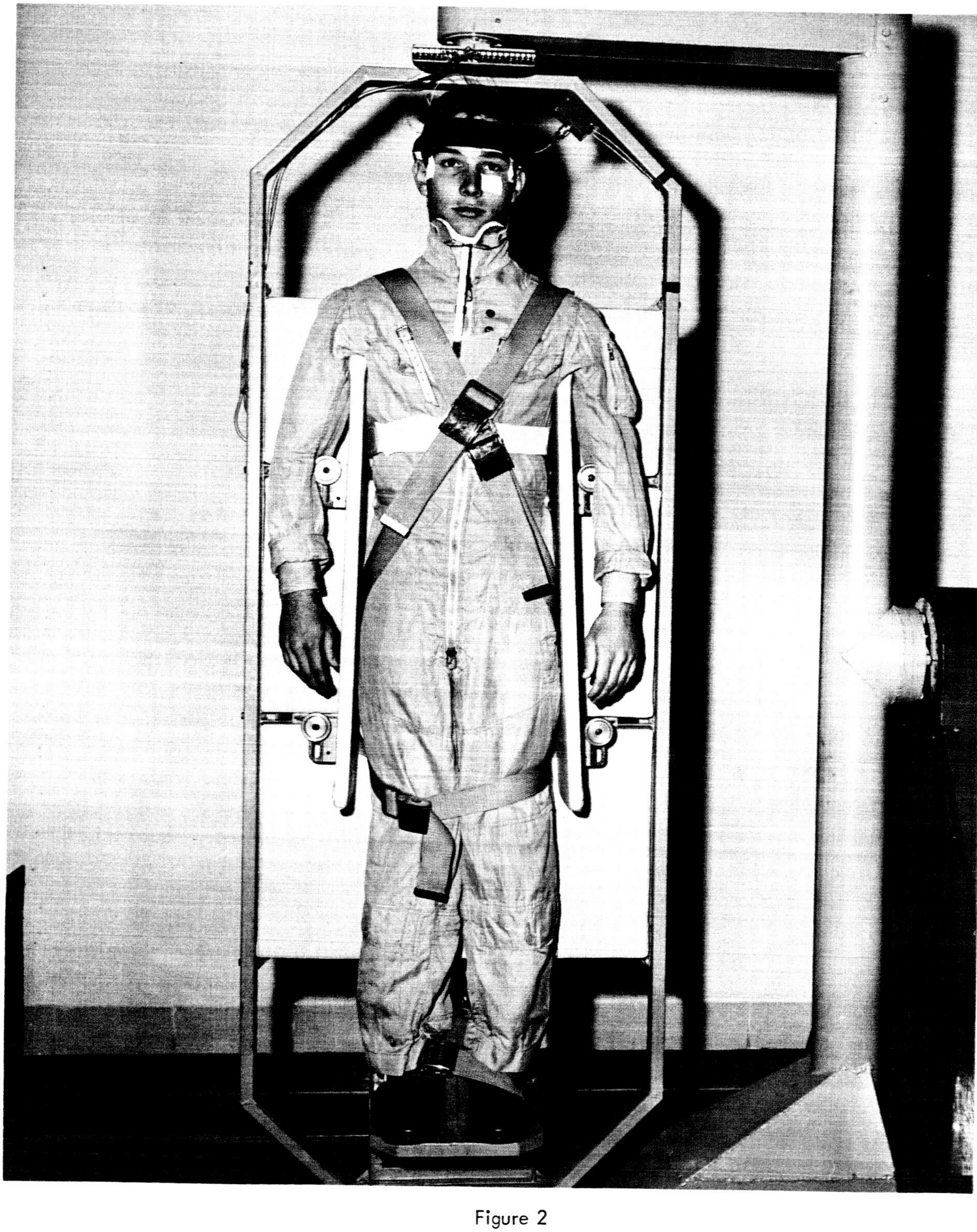

Figure 2

Subject Positioned to Spin about the Vertical Axis with Support Straps and Orthopedic Brace Visible

Salient features of the results of tests (Table I) with the axis of rotation horizontal were:

Nystagmus

(1) Typically, nystagmus during rotation persisted as long as the rotation continued, usually a period of two minutes. In some cases the rotation was maintained for three or four minutes, and nystagmus persisted throughout these longer intervals.

(2) Although nystagmus typically persisted throughout the period of rotation and always clearly persisted beyond its expected duration, it often diminished in intensity with time. Sometimes nystagmus diminished in intensity and quality for ten or fifteen seconds, and then a vigorous unidirectional response would recommence and persist for twenty or thirty seconds or until rotation stopped.*

(3) In some subjects the slow-phase velocity of nystagmus waxed and waned in a fairly fixed phase relation to the period of rotation, nystagmus being somewhat suppressed as the subject rotated through the nose-up position.

(4) In subject BU, nystagmus persisted throughout rotation# in one direction, CCW, but in the other direction of rotation, although the response commenced in the expected direction, it reversed directions after the first twenty seconds of constant angular velocity. This reversing nystagmus, first one direction, then the other, persisted throughout the period of rotation. This subject had a left-beating spontaneous nystagmus. When angular acceleration which commenced rotation was in a direction to facilitate the spontaneous nystagmus, the nystagmus response was essentially continuous during continuous horizontal-axis rotation. During CW rotation, when nystagmus began reversing, it reversed from the anticipated direction (nystagmus-right) to the opposite direction as the subject rotated through the nose-up position. Points of reversal were at the nose-up and nose-down positions. Another subject, MI, with spontaneous nystagmus gave similar results during horizontal-axis tests. Subject HU gave continuous nystagmus (which waxed and waned) and then a reversing nystagmus.

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* Probably relevant to this diminishing nystagmus were several aspects of the procedure: 1) subjects were not given mental tasks to artificially maintain arousal (6,8) during prolonged responses; 2) subjects were asked to think about sensations of bodily rotation, a mental set which may have led to nausea (8) which in turn is accompanied by loss of nystagmus (3, p.102). This is possibly due to a natural relationship between onset of nausea and drowsiness and nystagmus loss.

Response was essentially continuous for thirty-five seconds; then it waxed and waned for twenty-five seconds; then it was continuous for about thirty seconds, et cetera, but it never reversed directions.

Table I

Summary of Nystagmus and Subjective Data from Normal Subjects When the Axis of Rotation Was Horizontal. SP under Notes Indicates Spontaneous Nystagmus. Arrow to Reader's Left Means Nystagmus with Fast Phase to Subject's Left.

NORMAL SUBJECTS HORIZONTAL AXIS	CLOCKWISE					COUNTERCLOCKWISE			
	PER ROTATION		POST ROTATION			PER ROTATION		POST ROTATION	
SUBJECT	NYSTAGMUS	SENSATION	NYSTAGMUS	SENSATION	NOTES	NYSTAGMUS	SENSATION	NYSTAGMUS	SENSATION
CR	CONTINUOUS	CONTINUOUS	SHORT	NONE		CONTINUOUS	CONTINUOUS	SHORT	NONE
PA	CONTINUOUS	CONTINUOUS	SHORT	NONE		CONTINUOUS	CONTINUOUS	SHORT	NONE
BU	REVERSING	SHORT then	LONG	NONE	SP ←	CONTINUOUS	CONTINUOUS	SHORT	NONE
SU	CONTINUOUS	CONTINUOUS	SHORT	BRIEF PECULIAR SENSATION	NAUSEA	CONTINUOUS	CONTINUOUS	SHORT	NONE
Sch	CONTINUOUS W & W	CONTINUOUS	SHORT	NONE		CONTINUOUS W & W DIM	CONTINUOUS	SHORT	NONE
ZO	CONTINUOUS	CONTINUOUS	SHORT	NONE	NAUSEA SP →	CONTINUOUS W & W	CONTINUOUS	SHORT	NONE
GI	CONTINUOUS	CONTINUOUS	AVERAGE	NONE	NAUSEA	CONTINUOUS	CONTINUOUS	SHORT	NONE
BO	CONTINUOUS THEN W & W	CONTINUOUS 50 sec. then Oscillation	SHORT	NONE		NOT RUN			
AM	CONTINUOUS	FIRST then rocking sensation	SHORT	BRIEF COUNTER ROTATION		CONTINUOUS	CONTINUOUS	SHORT	BRIEF COUNTER ROTATION
PO	CONTINUOUS W & W	CONTINUOUS	LONG (45 sec.)	BRIEF COUNTER ROTATION		CONTINUOUS DIM		AVERAGE (35 sec.)	BRIEF COUNTER ROTATION
HU	W & W then REVERSING after 35 sec.	for 30 sec. then	AVERAGE	BRIEF COUNTER ROTATION	STOMACH AWARENESS	W & W REVERSING after 60 sec.	for 25 sec then	AVERAGE (29 sec.)	BRIEF COUNTER ROTATION
MI	CONTINUOUS for 54 sec. then REVERSING		AVERAGE (30 sec.)	BRIEF COUNTER ROTATION	STOMACH AWARENESS SP ←	CONTINUOUS W & W		SHORT — STRONG SECONDARY	BRIEF PECULIAR SENSATION

(5) Responses obtained from several normal subjects during rotation are shown in Figures 3 - 6 and illustrate some of the points mentioned above.

(6) Nystagmus produced by the deceleration from rotation about the horizontal axis was reduced in duration and intensity as compared with the post-rotational response produced by rotation when the axis of rotation was vertical.

Subjective Effects

(1) The sensation of rotation persisted throughout the duration of rotation about the horizontal axis in all except three of the normal subjects. One of these was BU who had spontaneous nystagmus and the reversing nystagmus during CW rotation. He reported a brief sensation of rotation during CW horizontal-axis rotation but a continuous sensation of rotation during CCW horizontal-axis rotation. Subject HU reported "nose-up, nose-down" rotation for about thirty seconds followed by confusion and then a cylindrical motion during which the nose maintained constant upward orientation.*

(2) Deceleration from horizontal-axis rotation did not produce a sensation of rotation in the opposite direction in most of the normal subjects. Five of the twelve normal subjects reported very brief sensations following rotation, which did not always involve a feeling of rotation. All others simply felt that they stopped; the post-rotational sensation of rotation was absent.

(3) Five of twelve normal subjects reported nausea or stomach awareness when they rotated about the horizontal axis. In another experiment (15) in which eighty subjects received eighty periods of rotation about a vertical axis within four hours, none reported nausea.

Effects of Error Introduced by the Rotary Device

The constant angular velocity during rotation about the horizontal axis was not really constant, due to imperfect counterbalancing. This produced a sinusoidal variation in velocity, with a minimum being reached as the subject was being raised to nose-up position and maximum attained as the subject rotated toward nose-down position. The variation in angular velocity was 1.0 deg/sec; period of the sinusoidal variation was 5.3 seconds. In order to determine whether this could account for the prolonged responses around the horizontal axis, the angular acceleration and angular velocity profiles were duplicated on a vertical axis device (Stille-Werner chair). Subjects who exhibited prolonged reactions around the horizontal axis on the electric posture table did not exhibit prolonged reactions during rotation

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* HU also exhibited reversing nystagmus after a time at constant rotation with the axis horizontal.

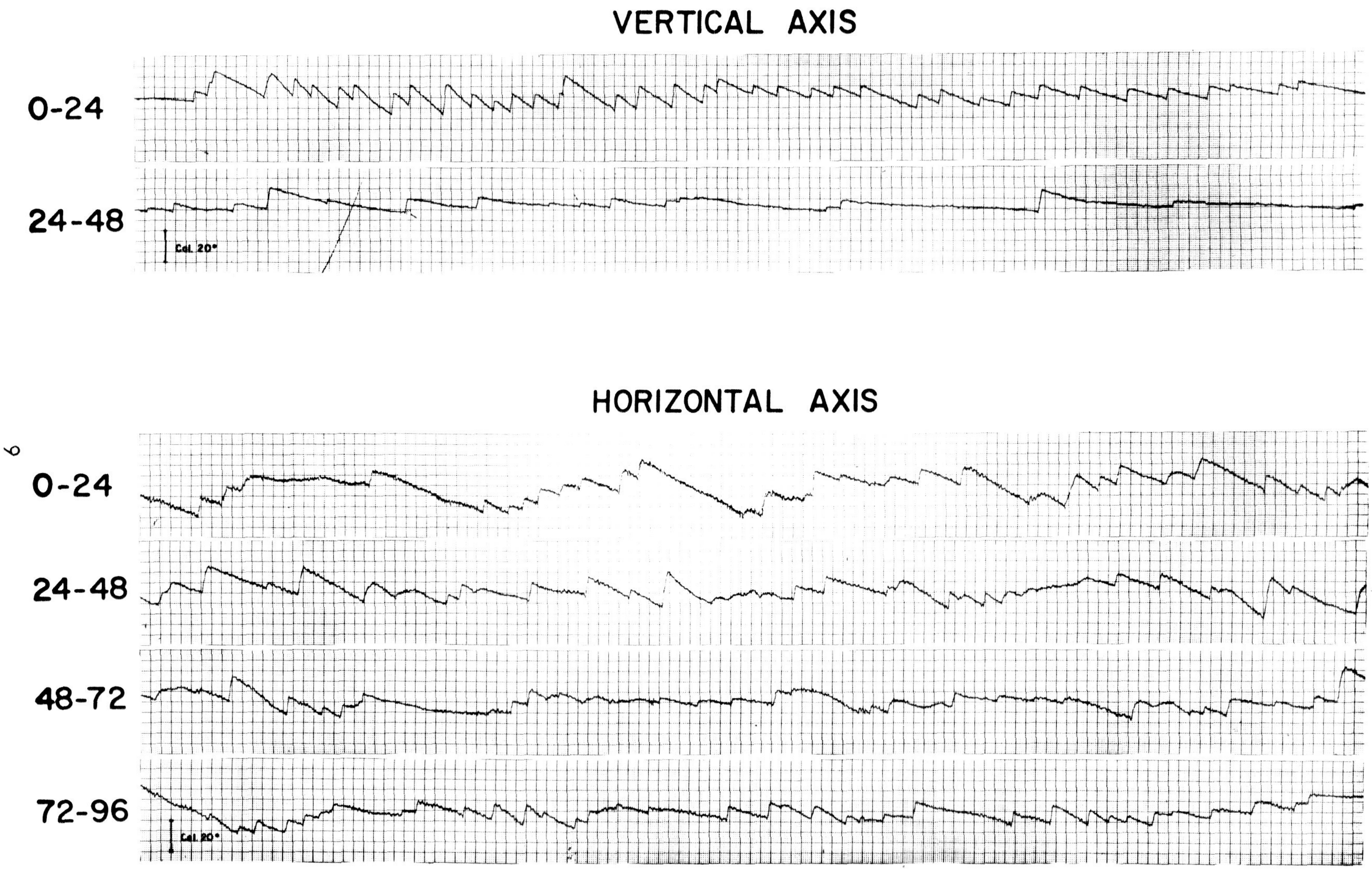

Figure 3

Showing Nystagmus Produced by Vertical and by Horizontal-Axis Rotation. This Subject Had an Unusually Long Response to Both Conditions but the Horizontal-Axis Clearly Produced the Longer Response.

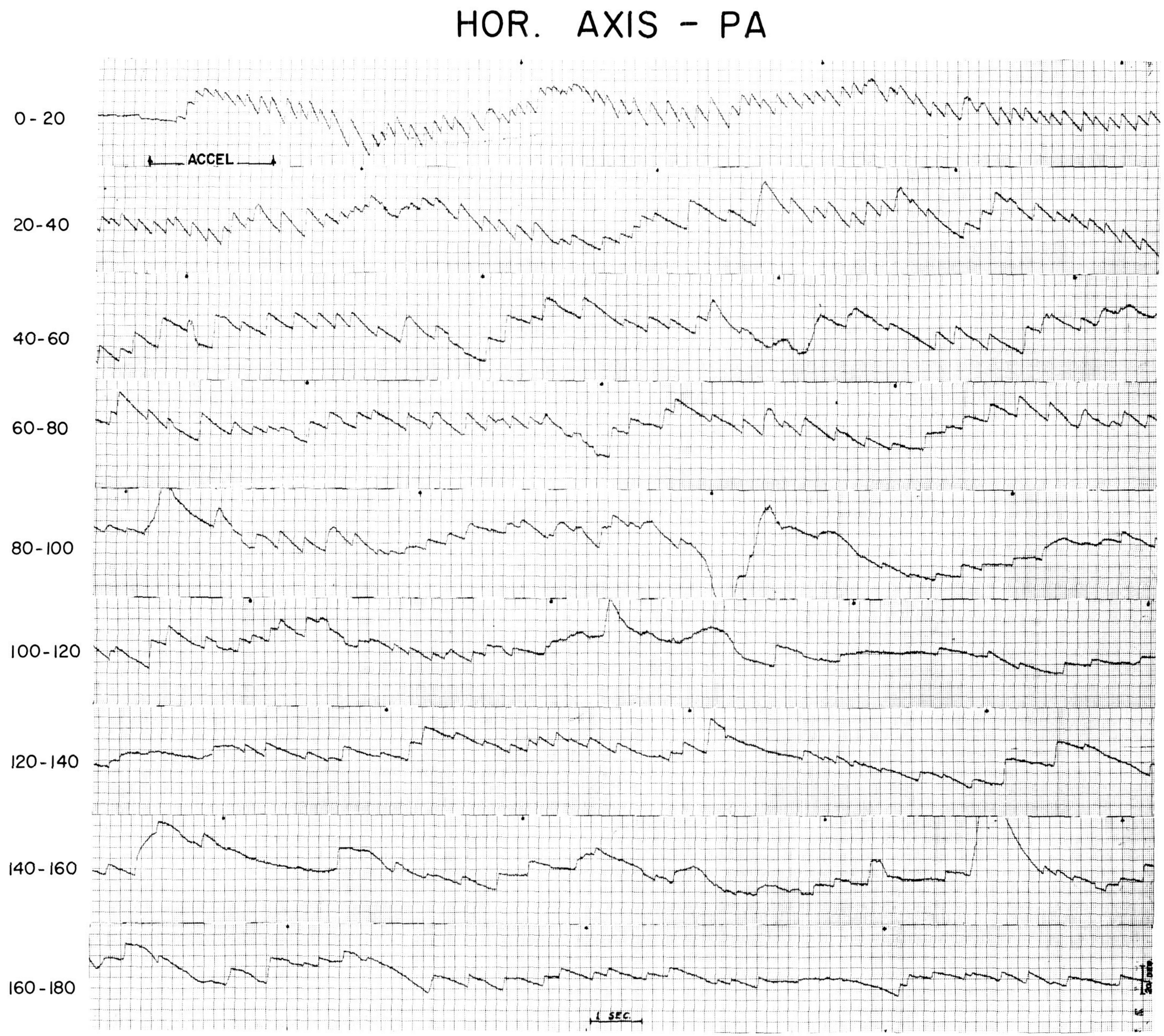

Figure 4

Nystagmus Produced during Rotation When the Axis Was Horizontal. The Response Persisted until Deceleration Commenced (220 Seconds). Dots on the Upper Portion of the Records Mark Rotation through the "Nose-up" Position of the Subject.

HOR. AXIS - AM

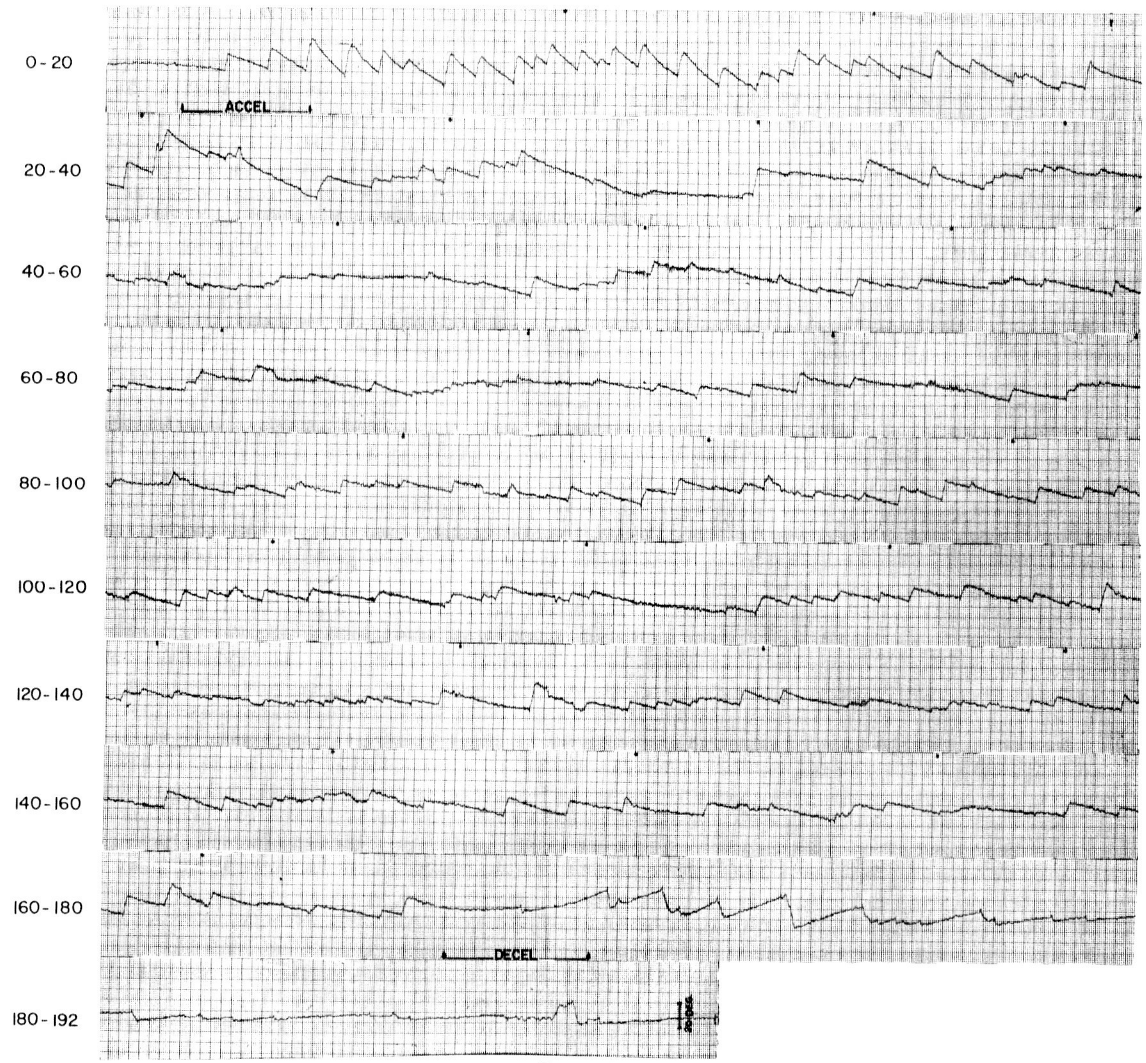

Figure 5

Nystagmus Produced during Rotation When the Axis Was Horizontal. The Response Continued for 167 Seconds at Which time Deceleration Was Commenced. The Brief Response to Deceleration Was Typical for This Orientation of the Rotation Axis. Dots on the Upper Portion of the Records Mark the Point at Which the Subject Rotated through the "Nose-up" Position.

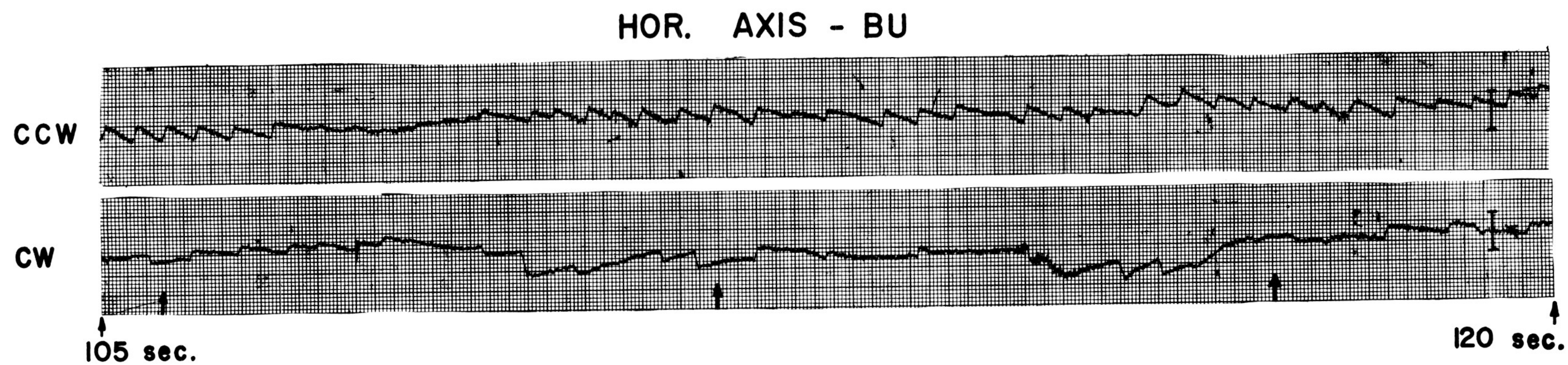

Figure 6

Showing the Different Types of Responses Obtained from Subject BU to the Two Different Directions of Rotation When the Axis Was Horizontal. Response Is Shown between t=105 Seconds and t=120 Seconds. Arrows on the Lower Part of the CW Record Mark the Point at Which Subject Rotated through the "Nose-up" Position.

on the vertical-axis device. It is concluded that these variations in constant velocity were not the cause of the prolonged reactions during horizontal-axis rotation.

LABYRINTHINE DEFECTIVE SUBJECTS

Tests with the axis of rotation vertical did not yield nystagmus or subjective effects in L-D subjects similar to the responses of normal subjects under the same conditions. Five of the eleven L-D subjects exhibited some nystagmus, but in four of these cases, the nystagmus was spontaneous; i.e., nystagmus was of the same direction irrespective of the absence, presence, or direction of stimulation. In all cases the nystagmus was very weak and usually of poor quality. One subject, PI, showed low order nystagmus during clockwise and counterclockwise accelerations which was, in each instance, appropriate to the directions of acceleration. However, these were very weak responses (2 - 4 beats with slow phase velocity of the order of 1 - 2 deg/sec), and these responses, elicited with the rotation-axis vertical, might have been overlooked except that PI was the only L-D subject whose reactions approximated the normal range of responses during the horizontal-axis tests.

None of the L-D subjects reported sensations of rotation during the vertical-axis tests.

Tests with the Axis of Rotation Horizontal (Table II)

Nystagmus. Only one of the eleven L-D subjects, PI*, showed a nystagmus response which approximated responses of normal subjects. A strong, right-beating nystagmus commenced immediately after 68 deg/sec CW angular velocity was achieved. This response persisted during constant angular velocity for more than 100 seconds (until deceleration commenced) but response intensity diminished with time, and waxing and waning of response was noticeable toward the end. During counterclockwise rotation, a left-beating nystagmus of poor quality appeared. This response was of lower intensity, poorer quality and less persistent than the response during clockwise rotation, but it was directionally appropriate to the rotational stimulus.

None of the other L-D subjects showed nystagmus responses typical of normal subjects during horizontal-axis rotation. Six L-D subjects showed either low order spontaneous nystagmus which was unchanged by the stimulation or no nystagmus at all. Three other L-D subjects showed fairly clear nystagmus which reversed directions throughout the periods of rotation. The remaining L-D subject showed a reversing nystagmus of very poor quality during rotation. Deceleration from horizontal-axis rotation failed to yield nystagmus in any of the L-D subjects.

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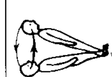
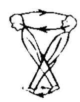
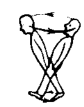
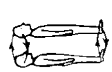
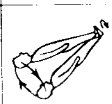
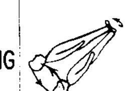
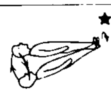
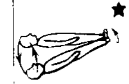
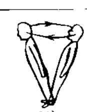
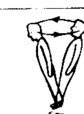
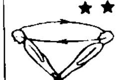
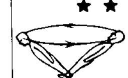
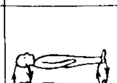
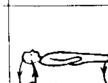
* PI, aged 23, lost hearing at age of 3 years due to meningitis. He has no hearing in either ear, and ice water caloric tests failed to produce nystagmus.

Table II

Summary of Nystagmus and Subjective Data from L-D Subjects When the Axis of Rotation Was Horizontal. SP under Notes Indicates Spontaneous Nystagmus. Arrow to Reader's Left Means Nystagmus with Fast Phase to Subject's Left.

LABYRINTHINE-DEFECTIVE SUBJECTS
HORIZONTAL AXIS

SUBJECT	CLOCKWISE PER ROTATION NYSTAGMUS	CLOCKWISE PER ROTATION SENSATION	CLOCKWISE POST ROTATION NYSTAGMUS	CLOCKWISE POST ROTATION SENSATION	NOTES	COUNTERCLOCKWISE PER ROTATION NYSTAGMUS	COUNTERCLOCKWISE PER ROTATION SENSATION	COUNTERCLOCKWISE POST ROTATION NYSTAGMUS	COUNTERCLOCKWISE POST ROTATION SENSATION
DO	REVERSING		NONE	NONE	SP → W	REVERSING		NONE	NONE
GR	POOR QUAL. REVERSING		NONE	NONE		POOR QUAL. REVERSING		NONE	NONE
GU	SP →		SP → VW	NONE	SP →	SP → VW		SP →	NONE
HA	→	★ 	NONE	NONE		→	★ 	NONE	NONE
JO	REVERSING		NONE	NONE		REVERSING		NONE	NONE
ST	SP →	★ 	SP →	NONE	SP →	SP →	★ 	SP →	NONE
PE	REVERSING		NONE	NONE		REVERSING		NONE	NONE
ZA	SP ←	★★ 	SP ←	NONE	SP ←	SP ←	★★ 	SP ←	NONE
MY	NONE	★ 	NONE	NONE		NONE	★ 	NONE	NONE
LA	WEAK RIGHT BEATING NYSTAGMUS		NONE	NONE		NONE		NONE	NONE
PI	CONTINUOUS RIGHT BEATING NYSTAGMUS		NONE	NONE		WEAK QUESTIONABLE LEFT BEATING		NONE	NONE

Subjective Effects. The subjective phenomena reported by the L-D subjects showed a remarkable range of variation, but there were also significant consistencies. During rotation about the horizontal-axis the subjects were intellectually aware of the true motion. Yet most L-D subjects perceived motion in which their bodies traced a conical path with the feet near the vertex. In some cases the vertex pointed downward, in others, upward, and in still others, the long axis of the cone was nearly horizontal. Several L-D subjects reported that the body traced a cylindrical path. However, perhaps the most significant and consistent fact reported was that all except two of the L-D subjects did not experience true rotation. For example, those L-D subjects who reported body motion in a cylindrical path said that the nose always pointed upward. Some said that during the very first revolution they experienced rotation, but thereafter, the nose always maintained about the same heading while the body traced the cylindrical or conical path. Only two of the L-D subjects, PI and GU, reported true rotation about the horizontal axis similar to that reported by normal subjects. Most of the L-D subjects expressed surprise at the perceived motion since they were intellectually aware of the true motion. None of the L-D subjects reported nausea.

(Tables I and II summarize the results obtained from normal subjects and L-D subjects in the tests conducted with the rotation axis in the horizontal position.)

One subject, not included in the tables, was known from previous experiments to have a strong directional preponderance. A low magnitude angular acceleration (1 deg/sec^2) was used to attain 68 deg/sec rotation in the CCW direction. When the axis of rotation was vertical, nystagmus and the sensation of rotation were absent. When the axis of rotation was horizontal, a vigorous nystagmus was produced and the sensation of rotation was present. The same stimulus magnitudes in the other direction of rotation (CW) produced nystagmus and sensations of rotation in both vertical and horizontal-axis tests, and again the reactions to the horizontal-axis test were more vigorous.

DISCUSSION

During constant angular velocity when the axis of rotation is horizontal, the cupula, if it is not influenced by gravity, should return to its position of static equilibrium in about thirty seconds by virtue of its elasticity (9). If the cupula is influenced by gravity, then during rotation about a horizontal axis, the restoring spring action of the cupula would be alternately hindered and aided by gravity. Under this circumstance it seems reasonable to anticipate a waxing and waning of the response during the cupula's return toward the position of static equilibrium, and this should be followed by a nystagmus which would reverse directions as gravity would drive the cupula back and forth on either side of the "null zone."

Results with normal subjects did not support either of these possible modes of response. The continuous nystagmus obtained from some of the normal subjects suggests that some other body system which is influenced by continuous reorientation relative to gravity is capable of maintaining the nystagmus initiated by the cupula deflection during angular acceleration.

The fact that individuals without labyrinthine function did not exhibit the continuous nystagmus typical of normal subjects indicates that a functional vestibular system is a necessary condition to this particular response. It may mean that the otolith system under this special circumstance is capable of producing or at least maintaining nystagmus. This is not, however, the only possible inference; for example, the results could also mean that once the canals have initiated the nystagmus (and the sensation), then the otoliths (or even other body systems) are capable of maintaining the nystagmus. Hence, the otoliths and/or other body systems (4) may be necessary for the continuous response, but by themselves may not be sufficient to elicit the response. These questions cannot be resolved on the basis of the present experiment.

The possibility that the stimulation of the otolith system may produce nystagmus has been examined by a number of investigators (4,20,33,34,35,36,37). Jongkees and Philipszoon (19) described nystagmus produced on a parallel swing which, assuming that the head was adequately fixed, precluded stimulation of the semicircular canals by angular acceleration. The author (7, 17) has observed nystagmic movements on the parallel swing, particularly when subjects were alert. Recently, eye movements with some of the characteristics of vestibular nystagmus have been ascribed to otolith function during vertical linear oscillation (28), and the triggering of positional alcohol nystagmus has been attributed to the otoliths although it is possible that canal function is also important (3; Money, personal communication).

Most studies which would deny that otolith stimulation produces nystagmus have involved a "static" rather than a dynamic stimulus. In other words, the otolith planes were positioned relative to gravity,and _after positioning_, the eyes were observed to determine whether or not nystagmus occurred. In such experiments, eye displacement was observed but nystagmus was not reported (31), except in individuals with positional nystagmus (3). The same is true for those experiments which involved direct surgical manipulation of the otoliths (41,43). It is important to note that with the parallel swing and with rotation around the horizontal axis, the stimulus involves change of linear acceleration rather than acceleration _per se_. With parallel swings: a) the direction of the resultant would change continuously relative to the otolith planes; b) the canals presumably would not be stimulated at all (18,21); and c) normal subjects report velocity sensations (16,46,47). Possibly stimuli which maintain the otolith system in a state of motion yield both velocity sensations and nystagmic eye movements when subjects are alert. Lowenstein and Roberts (26) noted neural activity in some units which seemed related to change in position rather than position _per se_*.

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* hence change in linear acceleration rather than acceleration, g, _per se_.

During continuous horizontal-axis rotation, nystagmus of otolith origin could consist of a slow phase which is the same as counterrolling with saccadic ocular repositioning due to the continuous reorientation of the otolith planes relative to gravity. In other words, when the eyes have counterrolled and stimulation continues, a saccadic movement repositions the eyes to permit continuation of counterrolling.

In most natural movements in which the head is tilted, the otolith system would be responding to changing linear acceleration and would provide information which is complementary to that initiated by the canals and other kinesthetic receptors. The functional value of this complementary pattern of sensory input should not be overlooked. The canals alone cannot indicate axis of rotation of the head relative to gravity. Theoretically (assuming that the canals are at best insensitive linear accelerometers) the same pattern of canal input can be produced by rotation around any of a variety of rotation axes. Hence, the canals and the otoliths would be necessary to indicate a plane of rotation relative to the earth; the otolith system would ordinarily indicate the axis (or plane) of rotation while the canals would indicate direction and magnitude of angular velocity. Once a position of tilt is attained with natural head movements, canal responses would cease and the otoliths, for a while at least, would indicate position relative to gravity.

The possibility that the otoliths may modulate the sensory information being transmitted to the higher centers from the canals has been suggested by a number of authors (25,30,32,42). Most experiments in which centrifugal force has been shown to modify "canal" responses can be interpreted either as a modulation of cupula-initiated responses by the otolith system or as an indication of cupular sensitivity to linear acceleration. In a recent experiment (22) it has been shown that the orientation of the subject relative to 1 G centrifugal force during equivalent angular accelerations influences the magnitude, the plane, and even the direction of nystagmus. Responses were observed which became directionally opposite to the anticipated reaction soon after the 1 G centrifugal force was attained.

Since the positional nystagmus of some individuals may be attributable to a cupula-sensitivity to linear acceleration (40), it is possible that both explanations are applicable but to a different degree in different individuals. In such cases, the otolith system could serve to correct erroneous information from the canals. In the present experiment, deceleration of normal subjects from horizontal-axis rotation produced "post-rotational" nystagmus in the anticipated direction, indicating cupula stimulation, but little or no post-rotational sensation. This lack of sensation suggests that data from other senses, signaling the cessation of rotation, suppressed (or modified) the cupula input at some level in the nervous system.* The nystagmus which was present at this time was reduced as compared with the post-rotational

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* Possibly related to this finding is the lack of turning sensation during certain centrifuge experiments reported by Bergstedt (3).

response following vertical-axis rotation. Subjects were stopped in a "nose-up" position. On the basis of subsequent experiments (8,29), in which responses produced by stopping in nose-up and nose-down positions were compared, it seems unlikely that these differences in post-rotational nystagmus in the present experiment (comparing vertical and horizontal-axis tests) are attributable either to arousal effects or to an influence of gravity on the cupula per se. Hence, the modulation of cupula input by otoliths and other kinesthetic receptors seems to be a more plausible explanation of the abbreviated response after horizontal-axis rotation in normal subjects.

A noteworthy aspect of the present experiment was the fact that five of the twelve normal subjects reported nausea or stomach awareness after only two relatively short periods (two minutes) of rotation around a horizontal axis. Graybiel and Johnson (13) also encountered a high incidence of nausea with a similar stimulus situation, an eccentrically located counterrotating cab on a small centrifuge. Subsequent experiments involving four ninety-second periods of rotation around a horizontal axis produced slightly over 50 per cent nausea in pilot candidates (8). The nausea in this situation may be attributable to the continued otolith response after the cupula has returned to resting position, an unnatural and antisynergic pattern of stimulation. Furthermore, the variety of the experiences reported by the L-D subjects* indicates that the nonvestibular kinesthetic receptors may be a source of confusion during prolonged continuous rotation and hence also may conflict in normal subjects with information generated by the otolith system. However, two other possibilities should be mentioned: 1) A continuous reorientation of the otolith system and other gravity-sensitive organs may be conducive to sickness, with or without sensory conflict; and 2) the visceral contents were also being reoriented relative to gravity during horizontal-axis rotation.

Both nystagmus and the sensation of rotation were different when the axis of rotation was placed in different orientations relative to gravity in normal subjects. This means that prediction of reactions from the theoretical mechanics of the cupula-endolymph system will not be feasible until these unpredicted reactions are understood. Some situations in aerospace operations may produce much more or much less nystagmus and disorientation than would be anticipated on the basis of present concepts of cupula mechanics. The fact that sickness was produced in tests about the horizontal axis also illustrates the wisdom of a statement by the late H. M. Johnson to the effect that "No wise man commits extrapolation in public." Unfortunately, extrapolation will be necessary in estimating reactions in aerospace ventures which include conditions reproducible in earth laboratories. Hence, the results emphasize 1)

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* Note of caution: The L-D subjects used in this experiment have been repeatedly exposed to various experiments dealing with spatial orientation. It is possible that these subjects through training have become more introspective than the normal subjects used. This may contribute, in part at least, to the wide variety of reported experiences by the L-D subjects.

the practical importance of increasing our basic understanding of the vestibular system and its interactions with other sensory systems and 2) the desirability of increasing our range of experimental observations to check the accuracy of our theoretical predictions.

The variety of responses obtained from "normal" subjects and the differences in responses between normal and L-D subjects suggest the possible usefulness of this kind of test in clinical application. Further work investigating this avenue of application is in progress.

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